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BIOLOGY AND IMMATURE STAGES OF SNAIL-KILLING FLIES BELONGING TO THE GENUS *TETANOCERA* (INSECTA: DIPTERA: SCIOMYZIDAE) III. LIFE HISTORIES OF THE PREDATORS OF AQUATIC SNAILS

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ABSTRACT

The geographic distribution, life history, and larval feeding habits of ten species of*Tetanocera* that prey on aquatic pulmonate snails are presented. All species are generalist predators of a broad mix of aquatic pulmonate snails. Differences in phenologies are apparent. Seven species are univoltine, whereas three are multivoltine. Three species overwinter as pupae, one species overwinters as partially grown larvae, and four species pass the winter months as diapausing first-instar larvae within eggs.

KEY WORDS: Diptera, Sciomyzidae, *Tetanocera*, aquatic snails, life histories

INTRODUCTION

This is the third paper in a series devoted to the biology and immature stages of Nearctic species of malacophagous *Tetanocera*. The first paper (Foote, 1996*a*) reviewed the literature, presented materials and methods, and gave natural history information for two species, *T. fuscinervis* (Zetterstedt) and *T. silvatica* Meigen, associated with shoreline snails. The second paper (Foote, 1996*b*) gave natural history information on four species, *T. melanostigma* Steyskal, *T. oxia* Steyskal, *T. rotundicornis* Loew, and *T. spirifera* Melander, that feed on succineid snails. The present paper focuses on the natural history of ten species, *T. annae* Steyskal, *T. ferruginea* Fallén, *T. latifibula* Frey, *T. loewi* Steyskal, *T. mesopora* Steyskal, *T. montana* Day, *T. obtusifibula* Melander, *T. robusta* Loew, *T. spreta* Wulp, and *T. vicina* Macquart, whose larvae prey on pulmonate aquatic snails.

LIFE HISTORIES

Tetanocera annae Steyskal

Steyskal, 1938. Occasional Papers of the Museum of Zoology of the University of Michigan, 386:5.

Tetanocera annae is a Nearctic species (Knutson et al., 1986) that has been recorded from Ontario and New Hampshire, west to British Columbia and Montana, and south to North Carolina and Ohio (Fig. 1). In central New York and northeastern Ohio, adults were found most commonly in partially wooded swamps that contained some standing water throughout the year. They were rarely collected in swampy woodlands containing only vernal pools, and were relatively uncommon in open grass-sedge and cattail marshes. Further evidence that this species prefers more wooded sites is that all of the field-collected puparia were found floating at the water's surface in small stands of alders or willows bordering

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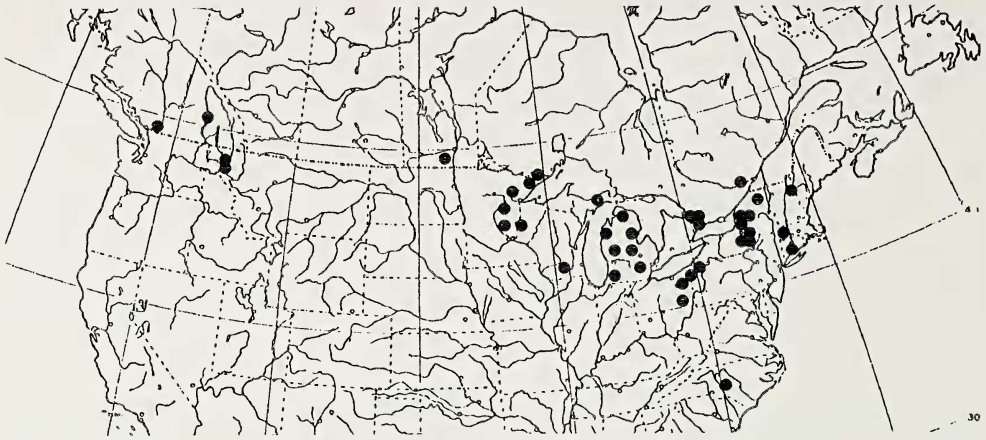

Fig. 1.—Distribution of *T. annae*.

open marshes. In contrast, the similar puparia of *T. ferruginea* were nearly always found in wetlands dominated by herbaceous vegetation.

Rearings of this species were initiated from two females collected on 21 August from the shaded marshy borders of a small woodland stream located near Oswego (Oswego County), New York. A more complete rearing was obtained from a female collected at the White Church marsh (Tompkins County) south of Ithaca on 3 July. Additional rearings were established from puparia collected in late March in an alder swamp near Ithaca.

Most of the nearly 500 eggs obtained in the laboratory rearings were scattered singly over the glass walls of the breeding jars, although a few were affixed to the cheesecloth covers. No eggs were placed on living or dead snails or on the peat moss that lined the bottom of the jars. The single female collected on 3 July deposited 379 eggs before dying on 11 August. Her last ten eggs were laid on 10 August. The incubation period lasted three to four days ($n = 51$).

In the rearing dishes, newly hatched larvae moved down to the water surface and broke through the surface film. The dichotomously branched interspiracular processes (float hairs) were obviously hydrofuge and served to keep the posterior end of the larvae in contact with the surface film. Therefore, the larvae are best considered to be infraneustic. Bubbles of air within the larval gut added buoyancy, and larvae held underwater quickly floated back to the surface film when released. A larva that was held continuously below the surface died within 20 minutes, suggesting that newly hatched larvae are not capable of foraging below the water surface.

At the surface film, larvae always came to rest against some support, usually the walls of the rearing dishes. Although they readily moved around the edges of the dish, they rarely ventured out into the open water. When larvae were placed in the open water, they quickly moved toward the dish edge by rapid downstrokes of the anterior half of the body. These observations suggest that in nature, the larvae lie in contact with floating debris or rest against emergent vegetation penetrating the water surface.

Larvae were predacious and showed no obvious preference for any particular species of pulmonate snail. They readily consumed numerous individuals of *Lym-*

naea palustris (Müller), *Helisoma trivolvis* (Say), *Biomphalaria glabrata* (Say), *Physella gyrina* (Say), and *Oxyloma effusa* (Pfeiffer). Newly hatched larvae easily overcame small snails that were less than 5.0 mm in length but were usually unsuccessful in attacking larger individuals. In contrast, third-instar larvae attacked and consumed the largest individuals of *L. palustris* available (shell length, 20.5 mm).

Larvae seemed to locate potential prey by a series of random movements. When a larva came in contact with a living snail, it quickly located the exposed foot and attacked the flesh with swift downward thrusts of its mandibles (mouth hooks). Shortly thereafter, a dark mass of ingested food appeared in the larva's gut. Unless disturbed, the larva fed to repletion before abandoning its prey. If the snail was less than 10 mm in length and the larva in the second or third instar, the flesh of the prey was usually consumed entirely. On the other hand, smaller larvae feeding on larger snails frequently left some flesh in the shell. No snail that had suffered feeding damage was seen to recover, even when only a small fraction of its flesh had been consumed.

The first larval stadium lasted an average of five days; the second, about seven days; and the third, from eight to ten days ($n = 13$). Shortly before forming puparia at the water surface, larvae voided the gut, became quite inactive, and did not feed for at least two days before pupariating. Although 16 puparia were obtained in the laboratory rearings, only two adults emerged. One adult emerged in 17 days, but the second one required 37 days. The remaining pupae apparently entered diapause, as they did not produce adults during the two months they were held at room temperature.

The discovery of puparia in the field on 29 March (two) and 3 April (three) coupled with my failure to obtain emergence from puparia formed in the laboratory during the summer months is strong evidence that overwintering occurs as diapausing pupae. This is probably a univoltine species.

One of three puparia collected on 2 April in the alder swamp near Ithaca produced a female of an undetermined species of Ichneumonidae on 14 April.

Tetanocera ferruginea Fallén

Fallén. 1820. Sciomyzides Sveciae, 9.

Tetanocera ferruginea is a common species in both Europe (Rozkošný and Elberg, 1984) and North America (Knutson et al., 1986). In the Nearctic region it occurs across the continent from Newfoundland to Alaska and south to New Jersey, Illinois, and California (Fig. 2).

In central New York and in Idaho, this species occurred most commonly in emergent or shoreline vegetation bordering permanent ponds and marshes, and was especially abundant in unshaded grass-sedge and cattail marshes. It was uncommon in marshes whose standing water disappeared during the summer and was very rare in woodland swamps. In northeastern Ohio, this was a common species in open marshes that retained water throughout the year.

At Ithaca, rearings were initiated from material collected at Boole's Backwater and at the Inlet Valley, Floral Avenue, and White Church marshes (Tompkins County). In southern Idaho, a rearing was obtained from adults collected in an open grass-sedge-cattail marsh located near Hagerman (Gooding County). Ohio rearings were initiated from three females collected in a stand of emergent veg-

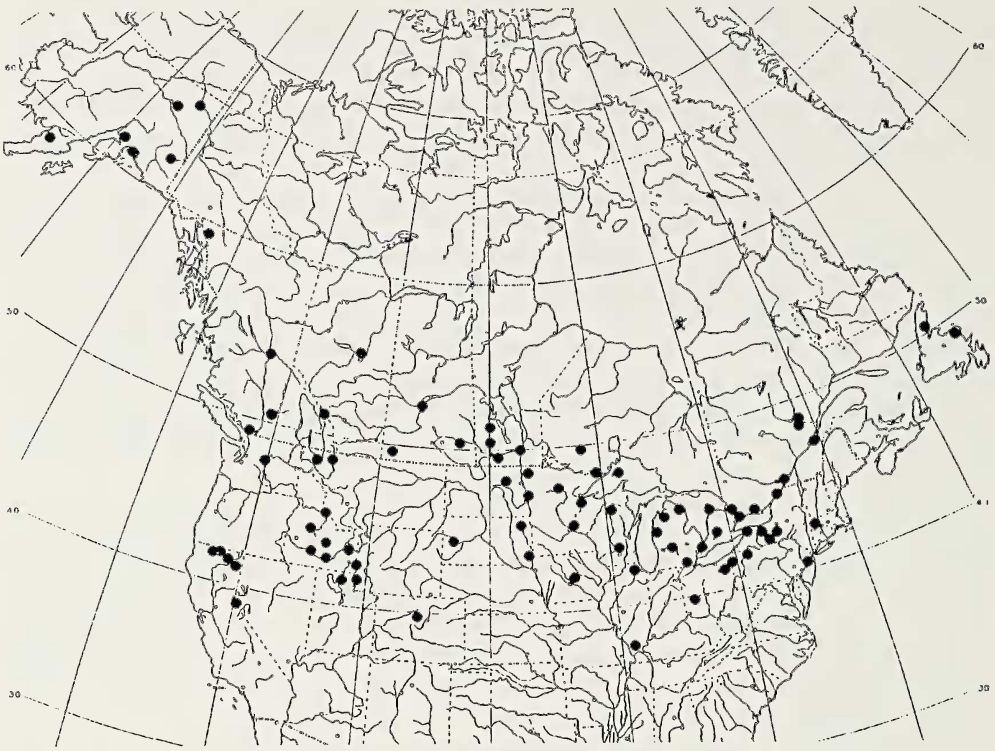

Fig. 2.—Distribution of *T. ferruginea*.

etation (*Sparganium, Juncus, Typha, Scirpus, Pontederia*) growing in the shallow water bordering Lake Hodgson (Portage County).

Females scattered most of their eggs singly over the glass walls of the breeding jars, but other eggs were placed on fragments of cattail and on projecting bits of sphagnum moss. A few were placed on the cheesecloth covers and a very few were laid on shells of living *Lymnaea* and *Helisoma* snails. Under laboratory conditions eggs hatched in four to six days (n = 100: Ithaca, 45; Hagerman, 40, Lake Hodgson, 15). Newly hatched larvae moved down the substrate until they encountered the surface film of the water in the breeding container. They then broke through the film and assumed a position on the underside of the film, retaining contact with atmospheric air via their spiracles that penetrated the film. No evidence was obtained that suggested that larvae can leave the surface to prey on completely immersed aquatic snails.

Larvae in nature were generalized predators of pulmonate aquatic snails. At Boole's Backwater, third-instar larvae were seen feeding on *Lymnaea palustris* and *Helisoma* sp. Laboratory-reared larvae consumed many individuals of *Lymnaea humilis* (Say), *L. obrussa* (Say), *L. palustris, Gyraulus parvus* (Say), *Helisoma anceps* (Menke), *H. subcrenata* Carpenter, *H. trivolvis, Biomphalaria glabrata, Planorbula armigera* (Say), *Physella gyrina* (Say), and *Aplexa hypnorum* (L.), as well as the terrestrial snails *Cionella lubrica* (Müller), *Zonitoides arboreus* (Say), *Catinella avara* (Say), and *Oxyloma effusa* (Pfeiffer).

Very few snails were able to evade an attacking larva. Occasionally a smaller

larva became trapped in the mucus produced by a large snail as it retreated into its shell, but larger second- and third-instar larvae were never observed to be trapped by this secretion. A specimen of *Biomphalaria glabrata* (diameter, 10.2 mm) showed a progressive slowing of the heartbeat during an attack by a nearly mature third-instar larva, and the heart action ceased within 18 minutes. Many large individuals of *Helisoma* bled profusely shortly after being attacked, indicating that their hemocoeles had been ruptured. Bleeding snails never recovered, even if the attacking larva was removed.

In the laboratory, the first larval stadium lasted four to six days; the second, three to four days; and the third, ten to 14 days (n = 44: Ithaca, 30; Hagerman, 14).

Fully grown larvae did not move into drier situations prior to pupation, and many puparia were obtained from larvae developing in dishes that contained only water and snails. When the substrate was moist paper toweling, as many puparia were formed above the toweling as below it. Very few of the larvae reared on moist sphagnum moss burrowed into it before pupation. The presence of float hairs and the upturned condition of the posterior end of the puparium indicate that this stage is adapted for floating. In nature puparia frequently were found floating in water several centimeters deep, usually in contact with debris or emergent vegetation. Adults crawled up onto the floating material or onto the vegetation before undergoing hardening of the body.

The pupal stage lasted nine to 12 days during the spring and summer breeding season (n = 33: Ithaca, 21; Hagerman, 12).

Mating began within a few days after females emerged from puparia. Females accepted males repeatedly, and copulation lasted from a few minutes to more than two hours. Mated, laboratory-reared females usually began ovipositing six to eight days after emerging. A female that emerged and mated on 13 May began ovipositing on 19 May. She laid from zero to 102 eggs daily between 19 May and 10 June, depositing a total of 535 eggs. There was a gradual decline in productivity after the first five days. Thus, between 19 May and 22 May an average of 60 eggs was laid daily, but from 23 May to 10 June the average dropped to 18 daily. The female died on 12 June, having lived for 30 days.

During oviposition, females moved slowly over the substrate while frequently applying the tip of the abdomen to the moss, cattail, or glass wall. Eggs were laid individually, and each egg-laying act took less than two seconds. Eggs were not laid in compact masses as has been observed for *Sepedon* (Neff and Berg, 1966), but were scattered over the substrate.

In central New York, the earliest seasonal record for adults was obtained on 13 May; the latest, on 28 August, and capture records are nearly continuous between those dates. Larvae were collected on 25 June and 1 August at Boole's Backwater in Ithaca, on 12 August at the Inlet Valley marsh, and on 29 October at the Floral Avenue marsh. Puparia were taken during February, March, April, May, and November. In laboratory rearings during the summer season, one generation followed another with no delays in development, each life cycle requiring approximately 40 days. Adults frequently lived at least until the first of their progeny emerged as adults. There is no reason to suppose that longevity of adults is appreciably less or that development is much slower in nature, and these observations establish beyond doubt that this species should be placed in Group 1 of Soós (1958)—eurychrone species having long, interrupted flight periods and breeding continuously to produce several generations per year. However, Soós

placed *T. ferruginea* in Group 3 because he noted an interruption in the capture records of the pinned specimens in certain European museums. Interruptions in capture records may result merely from interruptions in collecting efforts, not from actual interruptions in the occurrence of adults in nature. This is the correct explanation of data presented by Soós on *T. ferruginea.*

This species overwinters in the pupal stage. The pupae evidently can survive even when frozen in the ice cover of ponds and marshes. Seventy-eight puparia collected from marshes in central New York during February, March, and early April produced adults in nine to 11 days after being brought into the heated laboratory. All of these were taken at least one month before the first adult was collected in the area, and some were taken more than three months before that date. The earliest record for puparia that produced adults was made on 10 February, 1955, at the Inlet Valley marsh. Although ice still covered the marsh, it became soft and flexible under an unseasonably warm sun during that afternoon. As the ice sagged under my weight, water collected on top of it, and six puparia of *T. ferruginea* (plus 18 puparia of other species) were found floating in this water. Undoubtedly the water that was forced up onto the ice as the ice was depressed must have escaped through the holes that had formed around the stems of emergent vegetation, as melting occurred first around these dark objects. Puparia typically float into contact with any object which thus breaks the surface film, and they must have been concentrated in such situations before the marsh froze.

Six species of Ichneumonidae, *Theroscopus pumilis* (Cresson), *Theroscopus* sp. A, *Theroscopus* sp. B, *Theroscopus* sp. C, *Mesoleptus* sp., and *Phygadeuon* sp., were reared from puparia collected in marshes near Ithaca. Each infested puparium produced only one wasp. During the spring of 1958, information was obtained on the percentage of puparia infested with ichneumonids. Forty-five puparia collected on 28 February at the Inlet Valley marsh produced 33 flies and seven wasps. Fifteen collected on 30 March at the Floral Avenue marsh produced seven flies and five wasps. Twenty-one collected on 2 April at the same marsh produced 11 flies and seven wasps. Eighteen taken on 3 April at the same marsh produced 12 flies and three wasps. Sixty-two collected on 5 April 5 at the Inlet Valley marsh produced 45 flies and 13 wasps. Thus, ichneumonid larvae infested 16 to 33% of the overwintering puparia. From the total of 161 puparia, 35 wasps were reared (21%). In each sample, the adult wasps emerged two to six days after the last emergence of flies.

Tetanocera latifibula Frey (= *hespera* Steyskal, 1959)

Frey, 1924. Notulae Entomologicae, 4:51.

Steyskal (1959) described *T. hespera* from material taken in western North America, but this author placed it in synonymy with *T. latifibula* (Steyskal, 1965). It is now known to occur both in Europe (Rozkošný and Elberg, 1984) and North America (Knutson et al., 1986), where it ranges from Iowa to California and north to Alaska (Fig. 3). Adults were taken most commonly in Idaho and Washington by sweeping emergent and shoreline vegetation bordering open, permanent ponds and lakes, but a few specimens were collected also from unshaded vernal marshes that became dry by midsummer.

A rearing was initiated with a female swept on 17 August from a dense stand of *Scirpus* sp. growing in about seven centimeters of water at a small, permanent

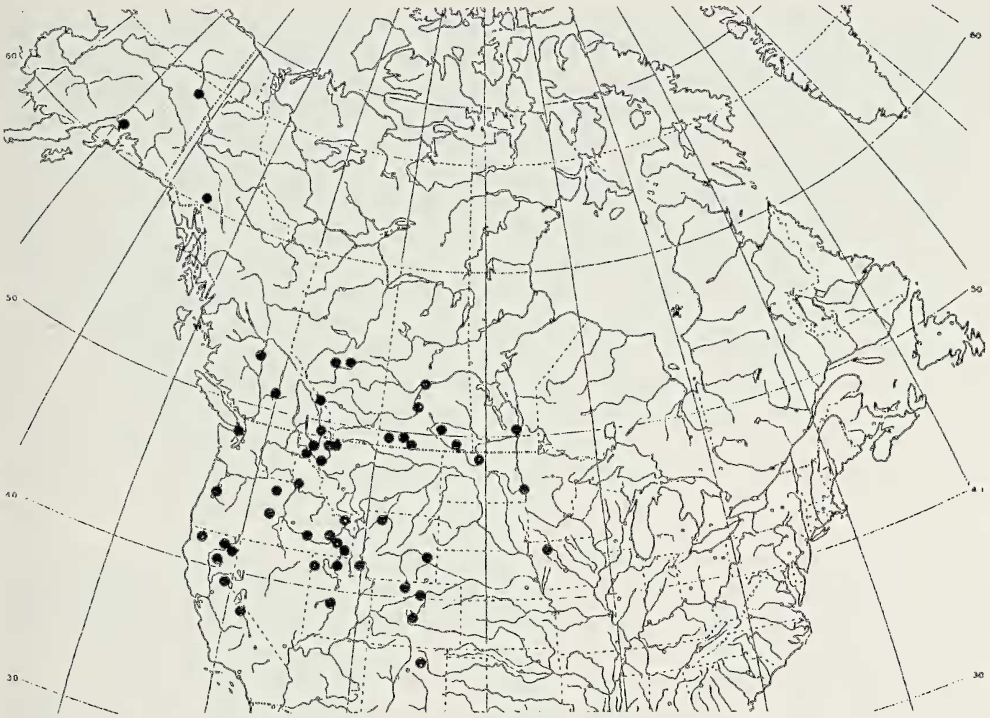

Fig. 3.—Distribution of *T. latifibula*.

lake located along State Route 18 about 33 km south of Sprague (Whitman County), Washington. She deposited 37 eggs on the cheesecloth cover of the breeding jar between 18 and 31 August.

Well-formed, living larvae were found when six eggs laid on 18 August were dissected on 31 August. These were transferred to a small amount of water and provided with several small *Helisoma* snails, but all remained very sluggish, did not feed, and died within five days. Hatching still had not occurred by 11 September, when the remaining 31 eggs were placed in a refrigerator and held at 7°C. Six apparently viable eggs were removed from the refrigerator and returned to the heated laboratory on 13 February. One egg dissected contained a living, first-instar larvae, which was placed in water and given a small *Physella*. The larva had not fed by 14 February, and was returned to the refrigerator. When checked on 16 February, this larva had consumed a 1.4- and a 2.7-mm-long *Physella* in the refrigerator. It was returned to the heated laboratory on 19 February, where it continued to feed on small *Physella*, consuming eight snails (1.4–5.0 mm long) while in the first instar, six (4.0–5.0 mm long) in the second, and 24 (2.9–10.0 mm long) in the third, for a total of 38 snails as a larva. The larva molted into the second instar on 24 February, into the third on 1 March, and finally formed a puparium on 20 March, 35 days after it was removed from the egg. During the four days preceding pupation the larva did not feed and remained relatively inactive. None of the other five eggs removed from the refrigerator on 13 February hatched, and all contained decaying remains of first-instar larvae when dissected on 1 March.

The remaining 25 eggs, only nine of which appeared viable, were removed from the refrigerator on 24 February. Two eggs were covered by mold and obviously dead. Fourteen had hatched in the refrigerator, but the larvae had not fed on the small, living snails included in the rearing dishes and were dead and badly decayed. Seven of the viable eggs were floated on a small amount of water and left at room temperature. The remaining two were dissected, and the larvae were removed. One of these first instars consumed six *Physella* (1.8–3.1 mm long) before molting into the second instar on 2 March. This larva fed on one additional snail before dying on 4 March. The second larva consumed five *Physella* (1.8–2.7 mm long) before dying on 1 March while molting into the second instar.

Two larvae that began to hatch on 24 February died before escaping from the egg envelopes. Three eggs hatched on 25 and 26 February, and on 2 March, but the remaining two never hatched and became covered by mold within ten days. Two of the three larvae that successfully emerged died while still in the first instar, although each fed at least once on small *Physella*. The larva that hatched on 26 February fed readily on *Physella*, molted into the second instar on 3 March, but died on 9 March. It consumed four snails (1.8–2.8 mm long) as a first instar and five more (1.5–2.6 mm long) as a second instar.

The only larva that pupated in the laboratory left the water on the preceding day, crawled up to the lid of the rearing dish, where it pupariated. The posterior end of the puparium was upturned, and the puparium floated when placed in water. A male emerged on 29 March, nine days after the puparium was formed.

The fragmentary rearing results indicate that *T. latifibula* has seasonal aspects similar to those of *T. loewi* (see below)—only one generation per year, with overwintering occurring either as eggs or as young larvae. Adults were taken in Idaho between 19 June and 3 August, but these dates probably do not indicate the entire flying season.

Tetanocera loewi Steyskal

Steyskal, 1959. Papers of the Michigan Academy of Science, Arts, and Letters, 44:68.

Restricted to the Nearctic Region (Knutson et al., 1986), *Tetanocera loewi* ranges from Ontario to North Carolina and Kansas west to Alberta and northern California (Fig. 4). In central New York and northeastern Ohio, adults and larvae were found most commonly in woodland swamps that contained vernal ponds. Although taken occasionally in open, vernal marshes, they rarely were collected in permanent marshes or along the marshy borders of unshaded lakes and streams.

Rearings were obtained from material collected in New York at the Inlet Valley marsh in Ithaca during early April (larvae taken by C. O. Berg), in a floodplain swamp along the outlet stream at Cayuta Lake (Schuyler County) during late August (adults), along the marshy borders of a sluggish woodland stream located near Oswego during August (adults), in a swamp woods near Albion (Orleans County) during April (larvae), and in the Manchester swamp (Ontario County) during April (larvae). Ohio rearings were initiated from three females collected on 20 September in a wooded swamp near Twin Lakes (Portage County).

In the breeding jars, eggs were scattered over the leaves of moss, the glass walls, and the cheesecloth covers. Very few of the eggs hatched, apparently being in diapause. Six eggs were laid on 29 August by a female collected on 24 August at Cayuta Lake. A larva that began to hatch from one of these on 10 September still had not escaped the egg on 12 September, when it was removed and placed

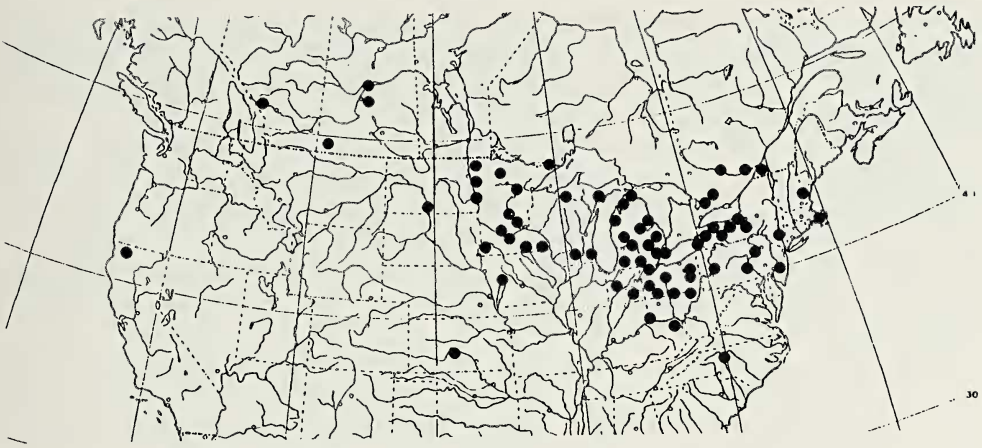

Fig. 4.—Distribution of *T. loewi*.

in several milliliters of water with several small *Helisoma* snails. The larva was very sluggish, did not feed even when placed on the expanded foot of a snail, and finally died on 18 September. On 18 September, the remaining five eggs were dissected, and four well-developed, living larvae were found. These larvae also refused to feed and all died within ten days. Twenty eggs laid on 17 September by another female from Cayuta Lake similarly failed to hatch, even though 16 of them contained well-formed, first-instar larvae when dissected on 5 October. These larvae remained inactive and failed to feed. During September, two females collected on 18 August near Oswego laid 55 eggs. A single larva emerged on 23 October, but did not feed and died on 29 October. No additional hatching was obtained, although many eggs contained living first- instar larvae when dissected on 1 November. None of these larvae fed on the small *Biomphalaria* and *Lymnaea* snails provided. Similar results were obtained with eggs deposited by females collected in late September in northeastern Ohio. The 57 eggs obtained were held at room temperature until fully formed, first-instar larvae were present. They were then treated in various ways in an effort to obtain hatching and feeding. Three eggs held continuously at room temperature for 107 days did not hatch. Ten eggs were placed in a refrigerator at 5–7°C for 15 days and then returned to room temperature. No hatching was obtained during the 50 days they were held at room temperature, and all had collapsed by mid-December. Additional sets of ten eggs were held in the refrigerator at 5–7°C for 30, 60, 90, and 129 days, respectively, before being returned to room temperature. No hatching occurred, although three larvae partially escaped the egg membranes. These larvae did not feed when extracted from the membranes and placed with small *Gyraulus* and *Physella* snails.

From the preceding results, it appears that embryogeny proceeds normally in eggs deposited in late summer and early fall, but the first-instar larvae remain within the egg membranes for an undetermined length of time. Hatching probably does not occur in nature until the larvae have been exposed to an extended period of low temperatures. Apparently, extended exposure to temperatures as low as 5°C is not sufficient to break the first-instar larval diapause.

Five first-instar and nine second-instar larvae were taken at the Manchester

swamp on 17 April. In contrast to the larvae obtained from laboratory-reared eggs, these free-living larvae fed voraciously on *Lymnaea palustris, Helisoma* sp., *Biomphalaria glabrata, Planorbula armigera*, and *Physella* sp., grew rapidly, and formed several puparia in the rearing dishes.

The five first-instar larvae molted into the second instar on 21 and 22 April, giving a first larval stadium lasting at least four or five days. The actual time spent as free-living, first instars probably was considerably longer as there was no way of determining when hatching had occurred. All five larvae molted into the third instar on 26 and 27 April, giving a second larval stadium lasting four to six days. Three larvae formed puparia on 9 May, giving a third larval stadium lasting about 12 days.

Although all puparia were formed beneath a layer of moist paper toweling, they floated at the surface when placed in water. The posterior end of the puparium was strongly upturned and float hairs were present, indicating that the puparia were adapted to floating. In the laboratory, the pupal stage lasted 15 to 19 days, adults being produced in late May (n = 10, Manchester swamp).

Females taken in the field during August, September, and early November accepted males repeatedly, with each copulation lasting five to 60 minutes. Six feral females collected in August and September each deposited seven to 40 eggs a few days after being confined to the breeding jars, but a lone female collected on 9 November at the Manchester swamp did not oviposit and died on 14 November. In contrast to females collected in late summer, laboratory-reared females and those taken in nature during June and July did not oviposit during the ten to 25 days they were in confinement.

Laboratory-reared females lived only ten to 15 days, but mortality could have been due to faulty rearing techniques. Feral adults collected in the summer months lived 20 to 25 days.

In central New York, adults were encountered between 5 June and 9 November. Flies were collected repeatedly between early June and late September. Overwintering apparently takes place either as first-instar larvae within eggs or as free-living, early-instar larvae. The earliest record for larvae was obtained by C. O. Berg on 9 April at the Inlet Valley marsh, and other first instar larvae were found as early as 17 April at the Manchester marsh.

The evidence summarized above demonstrates that *T. loewi* is univoltine. Second- and third-instar larvae and puparia develop in April and May, requiring averages of 5, 12, and 17 days for a total of 34 days to pass through these stadia. Adults emerge in late spring but apparently do not mate or oviposit until three months or more have passed. Although there might still be time for a second generation if the eggs produced in late summer and autumn developed directly, most of them do not and those that do develop produce only listless larvae that do not feed. A diapause seems to intervene usually just before, but apparently sometimes just after, hatching, and the first-instar larvae which are formed in August and September remain in that stadium until the following April (seven or eight months). Thus, the life cycle, which may be completed in as little as 45 days in multivoltine species of *Tetanocera*, is extended in *T. loewi* to several months. This extension is due to two long periods of suspended activity—the delay before adult flies mate and oviposit and the long period (either before or after hatching) during which the first-instar larvae do not feed.

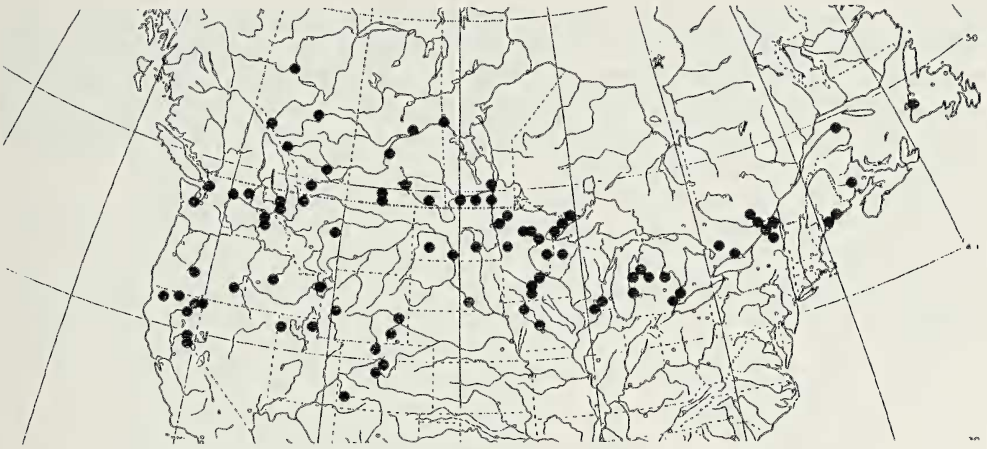

Fig. 5.—Distribution of *T. mesopora*.

Tetanocera mesopora Steyskal

Steyskal, 1959. Papers of the Michigan Academy of Science, Arts, and Letters, 44:70.

The known range of this strictly Nearctic species (Knutson et al., 1986) is transcontinental, extending from Newfoundland to British Columbia and south to New York, Colorado, and California (Fig. 5).

In northwestern Montana, adults were collected most commonly in open or partly shaded marshes dominated by species of *Carex*. In all marshes, there was a steady decline in water levels as summer progressed, and the habitats frequently lacked any standing water by late July. A few specimens were taken in more-permanent sedge marshes. Snails were abundant in all habitats and included species of *Gyraulus, Planorbula, Aplexa, Physella, Lymnaea*, and *Oxyloma*. Other species of Sciomyzidae commonly occurring with *T. mesopora* were *Atrichomelina pubera* (Loew), *Pherbellia anubis* Knutson, *P. griseola* (Fallén), *P. argyra* Verbeke, *Pteromicra siskiyouensis* Fisher and Orth, *Renocera cyathiformis* Melander, *Hedria mixta* Steyskal, *T. latifibula*, and *T. plebeja* Loew.

Rearings were initiated by a female collected on 10 August from a *Carex* marsh located along the Swan River about 8.8 km east of Big Fork (Flathead County), Montana, and by three females and two males collected on 25 August in a nearly dry sedge marsh situated some 11 km north of Deary (Latah County), Idaho.

The females collected on 10 August survived in the laboratory until 17 November but oviposited only on 19 August (nine eggs) and 13 September (12 eggs). Thirteen of these eggs were scattered over the cheesecloth covering the jars, and the remaining eight were attached to projecting sprigs of peat moss in the breeding jar. One egg hatched on 10 September, but the other 20 still had not hatched on 28 September when they were transferred to a constant- temperature chamber and maintained at a temperature of 22°C and long-day photoperiod (15 hours of light). Removal of the chorion of one egg of 29 September revealed a fully formed, first-instar larva. The larva was excised from the remaining egg membranes and placed in a small petri dish containing water and a few small aquatic snails. The larva remained sluggish, did not feed, and died on 5 October. Four of the remaining 19 eggs that had been placed at constant temperatures hatched within ten

days, and three newly hatched larvae began to feed on small aquatic snails. One larva did not feed and died seven days after hatching. The remaining 15 eggs had not hatched by 20 November when it was noted that all had collapsed, indicating death of the larvae. The scanty results presented here indicate that embryogeny proceeds normally in this species in eggs laid in late summer but that hatching is delayed until the following spring.

The three larvae that hatched in the constant temperature cabinet fed as overt predators on *Gyraulus parvus, Helisoma* sp., *Physella* sp., and *Lymnaea obrussa.* Each larva killed between nine and 13 snails (2.5–4.0 mm) as first instars, three to five (3.2–9.0 mm) as second instars, and seven to 15 (3.4–10.0 mm) as third instars. A few of the newly hatched larvae left the surface film to seek out submerged snails, but most maintained contact with the surface film via their posterior spiracles. The first stadium lasted seven to nine days; the second, four to five days; and the third, 28 to 33 days. No larva fed during the last two to three weeks of the third stadium and remained relatively inactive within the rearing dishes. One larva did not feed for 25 days prior to pupariation, and another did not feed for 18 days. The third larva died before forming a puparium. This long cessation of feeding by third-instar larvae is reminiscent of *T. plumosa* except that overwintering occurs as larvae in that species, with pupariation being delayed until the following spring.

One puparium was formed on 25 October; the other, on 13 November. Both puparia were held at room temperature until 2 December when they became moldy. Subsequent dissection determined that both pupae had died.

Two of the females collected on 25 August died on 11 September; the third female, on 20 September. They deposited a total of 142 eggs between 4 and 11 September. Very few of the eggs hatched, and no larva fed on the snails provided.

The rearing data are too few to allow definitive conclusions about the life cycle of this species, but it appears that there is only a single generation a year. Eggs probably are not deposited until mid- to late August; a lengthy diapause affects the fully formed, first-instar larvae within the eggs; and hatching in nature may be delayed until the following spring. The earliest collection date for adults was obtained on 5 June (Eaglebend, Minnesota); the latest, on 3 October (Mille Lacs, Minnesota).

Tetanocera montana Day

Day, 1881. Canadian Entomologist, 13:87.

Tetanocera montana is a Holarctic species (Knutson et al., 1986) that ranges in North America from Ontario west to Alaska and south to New York, Michigan, and Wyoming (Fig. 6). Adults and larvae were collected in central New York only at the Manchester swamp, where they were abundant among the emergent vegetation and floating plant debris of a vernal pond. In Idaho, adults were swept from emergent herbage and low shoreline shrubs bordering two small, shallow, but permanent, lakes that were partially shaded by overhanging trees.

Rearings were obtained from larvae taken at the Manchester swamp during April and from adults collected in a *Carex* sedge marsh bordering a small lake located some 11 km north of Fortine (Lincoln County), Montana, on 6 July.

Eggs laid in the laboratory always were scattered on the cheesecloth covers or on the upper three centimeters of the glass jars. The incubation period was strik-

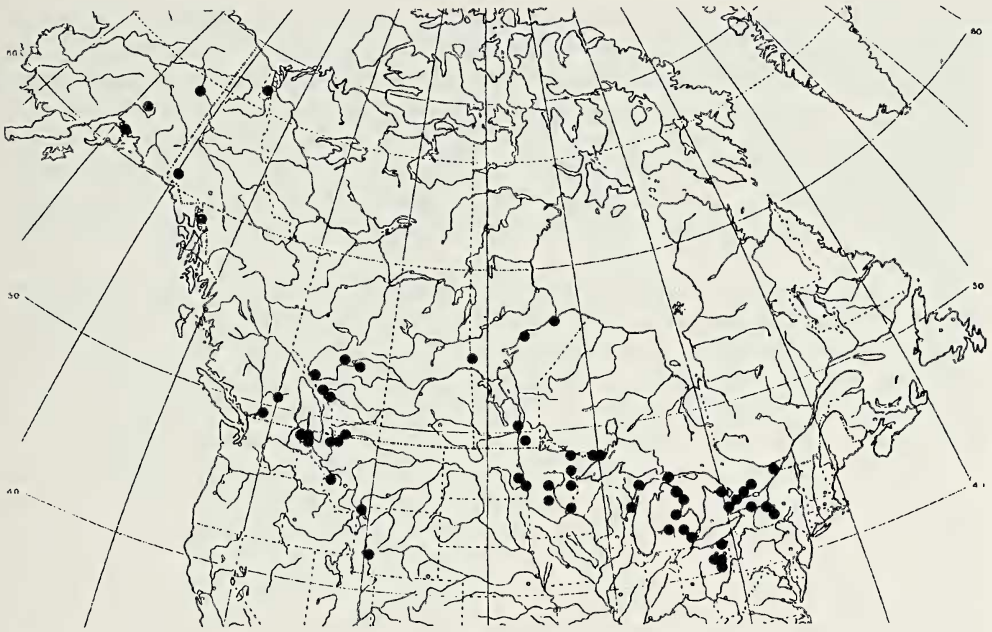

Fig. 6.—Distribution of *T. montana*.

ingly extended, and it appeared that eggs or, more likely, the first-instar larvae underwent diapause within the egg membranes before hatching.

On 13 June, 16 eggs laid by laboratory-reared females that had developed from larvae taken at the Manchester swamp were placed in small Stender dishes and left at room temperatures. Although embryogeny took place, only three larvae emerged. One of these emerged 23 days after the eggs were deposited, another after 25 days, and the third after 28 days. The three larvae were very sluggish, fed sparingly on *Australorbis*, and died within five days. Dissection of the remaining 13 unhatched eggs during late July disclosed that six contained well-developed, living, first-instar larvae, but the remaining seven eggs contained no larvae and were covered with mold. The six larvae excised from eggs were also very sluggish, rarely fed, and died within a few days. The unusually long incubation period of this species was very similar to other species developing in vernal woodland ponds (e.g., *T. loewi*).

Twenty-three eggs laid by females collected at the lake in Lincoln County, Montana, also failed to hatch during the 95 days they were held at room temperature, although one larva partially escaped from an egg before dying. All of the remaining eggs eventually became covered with fungi, an indication that the larvae had perished. Another 25 eggs were held at room temperature for 15 days and then transferred to a refrigerator where they were held for an additional 183 days. No hatching was obtained, although many eggs contained first instars.

Larvae collected in the field in New York were predacious and destroyed many individuals of *Lymnaea palustris, Helisoma* sp., *Australorbis glabratus, Planorbula armigera, Gyraulus parvus*, and *Physella* sp. At the Manchester swamp, second- and third-instar larvae were very abundant on the decaying leaves and stems of a coarse sedge floating in approximately 0.3 m of water during April.

Associated with them were many individuals of *T. loewi* and a few of *T. plumosa*. Aquatic snails such as *Lymnaea palustris, Physella* sp., *Planorbula armigera, Aplexa hypnorum*, and the succineid *Catinella avara* were abundant. Many of the *T. montana* larvae collected on 17 April were in the second instar, but most of the 30 larvae taken on 20 April were in the third instar. These larvae completed development rapidly in the laboratory and began pupariating during late April.

Under laboratory conditions the first larval stadium lasted three to four days; the second, four to seven days; the third, eight to 12 days ($n = 6$, Manchester swamp).

During the day preceding pupariation, many larvae ceased feeding, emptied the remaining gut contents, and became relatively inactive. They made little attempt to reach a drier situation, and most formed puparia in water that was five to ten millimeters deep. (The spiracular float hairs and the upturned posterior end of the puparium indicate that this stage is adapted for floating.) Under laboratory conditions, the pupal stage lasted 16 to 20 days ($n = 15$, Manchester swamp).

Three females that emerged on 17 and 18 May from material collected at the Manchester swamp were first seen copulating on 23 May. Copulation was repeated frequently thereafter, and each act lasted from 30 to 60 minutes. Two females began ovipositing on 20 June, the third on 23 June, 33 to 37 days after emerging. Before I killed them on 2 July, they each deposited between 23 and 30 eggs. A female collected at Westmond (Bonner County), Idaho, on 8 July began ovipositing on 10 July and laid a total of 116 eggs before dying on 18 July.

Larvae were collected only at the Manchester Swamp on 17 and 20 April. Adults were taken there during July and August. Because the laboratory-reared females delayed oviposition more than a month after emerging, it is probable that *T. montana* is univoltine. Overwintering probably occurs as unhatched eggs or young larvae, larval feeding occurs during late winter and spring, pupariation occurs in late April and May, and adults emerge in late May and early June.

Tetanocera obtusifibula Melander

Melander, 1920. Annals of the Entomological Society of America, 13:328.

Except for a doubtful record from the province of Quebec in eastern Canada, *Tetanocera obtusifibula* is known only from Idaho, Washington, Oregon, California, and British Columbia (Fig. 7). In Idaho, the only locality where the biology was studied, adults were found exclusively in vernal marshes that became dry by midsummer. Near Moscow in Latah County, they were swept in late summer from emergent plants (sedges, grasses, rushes) growing in unshaded, dry marshes. These marshes contained water up to 0.3 m in depth during the early spring, but as summer advanced, the water level dropped until by mid-July they lacked standing water.

On 7 April, two third-instar larvae were observed crawling about on floating plant debris in a very small, unshaded, vernal pond located just east of Moscow. Another third instar was taken on 20 April. The pond was only 3.1 m long and not more than 1.0 m wide at its broadest point. At the time of collection it was filled with water to a depth of 25 cm and was choked with immersed and emergent vegetation, mostly sedges and rushes, and supported a large population of *Lymnaea* sp. snails. The water level receded steadily during May, and by late June the depression was dry.

The two larvae collected on 7 April were placed in a refrigerator at 10°C and

Fig. 7.—Distribution of *T. obtusifibula*.

left there until 18 April when they were returned to room temperature. The larva collected on 20 April was not subjected to this cold treatment. At room temperature all three larvae were very active and fed daily on small *Lymnaea* taken at the pond. They ceased feeding on 28 April, emptied their gut contents, and became relatively inactive. They did not attempt to reach a drier situation, and on 29 April all puparíated at the water surface. Males emerged on 13 and 14 May and a female on 16 May, giving a pupal stage lasting 14 to 17 days. All three adults died within three days without copulating.

Females taken from June to early August did not contain recognizable eggs, but a female taken on 21 August contained a large number of well-developed eggs when examined on 8 September, the day she died. Two females collected in marshes near Deary (Latah County), Idaho, on 25 August were placed in breeding jars with males. Copulation was first observed on 26 August and was repeated frequently during the next ten days. They deposited 166 eggs on 4 September on the cheesecloth cover of the breeding jar. Thirty-seven of these eggs were held continuously at room temperature for 141 days. Eleven larvae attempted to hatch during this period, but only one larva completely escaped the egg membranes. It fed twice on small *Physella* snails before dying 15 days later. The remaining 26 eggs underwent embryogeny, with fully formed, first-instar larvae being formed, which never hatched and eventually collapsed. Another 85 eggs were held at room temperature for ten days without hatching and were then transferred to a refrigerator where they were held at 5–7°C for varying periods of time before being returned to room temperature or placed in a freezer at 0°C. Of 40 eggs held at 5–7°C for 170 days, 18 hatched while still in the refrigerator. However, none of

the newly emerged larvae fed. None of the remaining 22 eggs hatched after they had been returned to room temperature. No hatching occurred in 45 eggs that were subjected to 5–7°C for 40 days and to 0°C for 89 to 121 days before being returned to room temperature.

The records indicate that there is only one generation per year with overwintering occurring as larvae. Puparia are formed in late April or May, and adults emerge in late spring or early summer. Adults remain active throughout the summer, but do not begin ovipositing until late summer or early fall. Eggs undergo embryogeny and become first-instar larvae within a few days. However, larvae then go into diapause and do not escape the egg membranes until the diapause has been completed. Hatching possibly occurs in late autumn, but probably is delayed until early spring.

Parasitism by unidentified roundworms (Nematoda) was noted in two females of *T. obtusifibula* collected on 26 June in a small sedge meadow located two kilometers north of Deary, Idaho. Both females had greatly distended abdomens when collected. Four roundworms emerged from the abdomen of one female on 29 June; two, from the second female on 30 June. The abdomens of both females collapsed shortly after the worms had emerged, and both died a day later without ovipositing.

Tetanocera robusta Loew

Loew, 1847. Stettiner Entomologische Zeitung, 8:197.

Tetanocera robusta is Holarctic in distribution (Knutson et al., 1986), ranging in North America from Michigan and Ontario west to Alaska, and south to Utah and New Mexico (Fig. 8). In Idaho, adults were taken most abundantly in open, permanent marshes and along the unshaded borders of lakes. A few were swept from open, vernal marshes and a very few were taken in shaded marshes bordering small ponds.

A rearing was initiated on 8 August from eggs laid by a female collected the same day at Robinson's Lake, 15 km east of Moscow in Latah County, Idaho. Of the 175 eggs obtained from this female, 92 were laid on the glass wall of the breeding jar, 72 were affixed to the cheesecloth cover, and 11 were attached to a short length of *Typha* leaf. They were scattered over the substrate, and no clusters contained more than five eggs. Hatching occurred in three ($n = 44$) or four days ($n = 29$) under laboratory conditions.

Groups of eggs were subjected to different hatching conditions in efforts to determine whether eggs immersed in, or floating on, water will hatch and whether the eggs can withstand prolonged chilling. All but two of 24 eggs placed on a short length of microscope slide projecting above the water hatched. In contrast, only six of 24 that were floated on water produced larvae, and only one of 14 newly laid eggs that were completely immersed hatched. No hatching was obtained in 20 eggs that were immersed after being exposed to air for 48 hours. None of 20 eggs held in a refrigerator at 7°C for four months hatched when returned to room temperature. These results indicate that *T. robusta* eggs are not resistant to prolonged exposure to either wetting or low temperatures.

Records were kept of the number and dimensions of snails killed by the predacious larvae. Individual larvae in small, plastic petri dishes containing a small amount of water were given three or four living snails daily. Snails used were

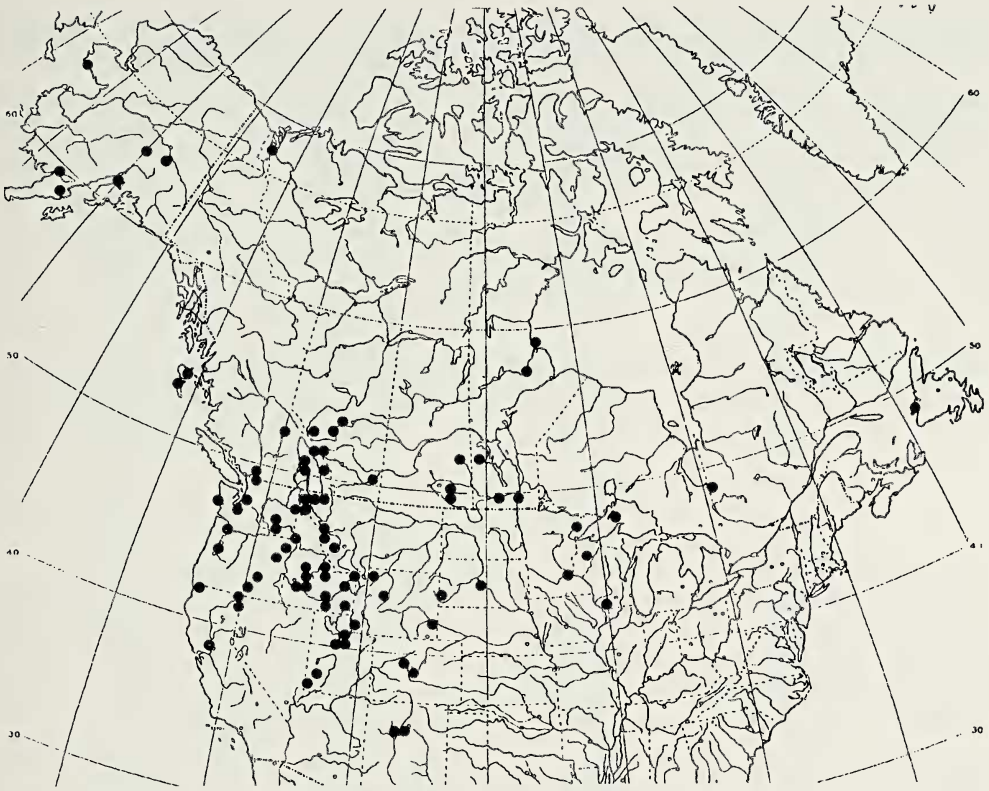

Fig. 8.—Distribution of *T. robusta.*

Gyraulus parvus, Helisoma subcrenatum, Lymnaea obrussa, and *Physella* sp. (Table 1).

Apparently the species of snail available does not influence the total number consumed by the larvae unless one species is considerably larger than the others. Larvae killed from 20 to 26 small *Gyraulus, Lymnaea*, and *Helisoma*, but only 12 to 16 larger *Lymnaea* and *Physella*. Larvae were placed individually in petri dishes containing different-sized *Lymnaea obrussa* or *Helisoma subcrenatum*. One snail was given to each larva. Larvae killed and fed upon *Lymnaea* that were five, eight, and ten millimeters long and *Helisoma* that were two, five, and six millimeters in diameter. These small larvae had considerable difficulty attacking snails greater than about eight millimeters in greatest dimension. To determine how long newly hatched larvae could survive without food, five larvae were placed on 28 August in small dishes containing only a slight amount of water. Four of these larvae died on 1 September, but the remaining larva lived until 3 September.

Larvae developed normally in water considerably deeper than their body lengths. They fed several times on *Gyraulus* in water that was ten and 20.0 mm deep. Mortality of larvae was no higher in the deep water than in water that was only two to five millimeters deep.

Under laboratory conditions the first larval stadium lasted from four to six days; the second, from two to seven days; the third, from six to 11 days ($n = 19$). The

Table 1.—*Numbers and dimensions (lengths of* Lymnaea *and* Physella, *diameters of* Gyraulus *and* Helisoma *in millimeters) of snails killed by larvae of* T. robusta. *Species of snail killed:* G. = Gyraulus parvus, H. = Helisoma subcrenatum, L. = Lymnaea obrussa, P. = Physella *sp.*

Larva	Snails consumed during			Total number of snails killed
	First instar	Second instar	Third instar	
1	7 *G.* (2.2–2.8)	6 *L.* (4.5–6.1)	12 *L.* (5.0–9.2)	25 (2.2–9.2)
2	10 *G.* (1.6–2.6)	5 *L.* (4.5-8.0)	8 *L.* (4.5–7.0)	23 (1.6–8.0)
3	11 *G.* (1.7–3.0)	4 *L.* (5.0–9.0)	8 *L.* 6.0–8.0)	23 (1.7–9.0)
4	10 *G.* (1.7–3.0)	6 *L.* (5.8–8.4)	8 *L.* 5.8–8.5)	24 (1.7–8.5)
5	9 *G.* (1.7–3.2)	4 *L.* (5.5–7.0)	10 *L.* (5.2–13.2)	23 (1.7–13.2)
6	8 *G.* (1.8–2.4)	7 *L.* (4.0–7.0)	10 *L.* (4.0–7.0)	25 (1.8–7.5)
7	10 *G.* (1.9–2.4)	4 *L.* (4.0–7.0)	12 *L.* (5.0–9.0)	26 (1.9–9.0)
8	7 *G.* (1.6–2.6)	5 *L.* (4.0–7.0)	12 *L.* (5.0–9.0)	24 (1.6–9.0)
9	8 *G.* (1.9–5.0)	2 *H.* (3.0–4.8)	10 *H.* (3.8–10.0)	20 (1.9–10.0)
10	8 *G.* (1.7–2.4)	5 *H.* (1.8–3.3)	9 *H.* (4.8–8.0)	22 (1.7–8.0)
11	8 *G.* (1.5–5.0)	6 *H.* (3.0–6.2)	10 *H.* (3.5–8.5)	24 (1.5–8.5)
12	3 *L.* (3.4–4.2)	6 *L.* (3.2–8.0)	7 *L.* (6.1–9.8)	16 (3.2–9.8)
13	2 *L.* (3.8–5.0)	2 *L.* (5.4–6.0)	8 *L.* (6.8–9.2)	12 (3.8–9.2)
14	2 *P.* (3.4–4.2)	5 *P.* (4.9–9.4)	8 *P.* (7.0–9.0)	15 (3.4–9.4)
15	3 *P.* (2.8–5.5)	5 *P.* (5.3–8.0)	7 *P.* (7.0–10.0)	15 (2.8–10.0)
16	3 *P.* (3.4–5.5)	5 *P.* (5.5–9.0)	7 *P.* (6.2–9.0)	15 (3.4–9.0)

day preceding pupariation, many larvae ceased feeding and became relatively inactive. Of the 22 puparia obtained in the laboratory, 12 were formed above the water on the walls of the rearing dishes and ten were floating at the water surface. Several adults were obtained from puparia formed in both situations. The pupal stage lasted from 12 to 16 days ($n = 7$). Records were not obtained on the number of eggs laid by laboratory-reared adults, but two field- caught females deposited 60 and 175 eggs, respectively, during the nine and eight days they lived in the breeding jars.

Information on seasonal aspects of *T. robusta* comes in part from subarctic regions. In Iceland, Nielsen et al. (1954) found young larvae on 20 July and in August; older larvae from 10 July to 12 August; mature larvae in August; and puparia in July, in August, and on 13 April. They suggested that "the species winters as mature larvae or puparia." A floating puparium collected at Fire Lake, near Anchorage, Alaska, on 26 June 1952, produced an adult fly on 1 July. Adults were taken commonly throughout the summer in Idaho. The earliest record is 17 May; the latest, 25 September. The entire life cycle was completed in 40 days in

Fig. 9.—Distribution of *T. spreta*.

Idaho, with no delays in development. This indicates that *T. robusta* has more than one generation per year at that latitude, although it probably is univoltine in more northern parts of its range.

Tetanocera spreta Wulp

Wulp, 1897. Biologia Centrali-Americana. Diptera, 2:358.

Tetanocera spreta is known only from southcentral Mexico (Knutson et al., 1986), where it has been recorded from Toluca (Michoacan), Jalisco (Jalisco), and Mexico City (District Federal) (Fig. 9). I am indebted to S. E. Neff for information on the biology of this species. A rearing was initiated from two females collected on 22 August 1958, by sweeping water hyacinth, cattails, and sedges growing abundantly in the shallow water of a roadside ditch located along Route 190 near Kilometer 15, District Federal, Mexico.

The females deposited 77 eggs between August 25 and September 15, with over half of the eggs being laid before August 28. Nearly all eggs were placed on the leaves and rhizoids of the moss present in the jar, but a few were attached to the glass walls of the container. Hatching occurred in three to five days under laboratory conditions. The larvae possessed sizeable float hairs and were obviously adapted to an aquatic existence. They fed upon the aquatic snails *Helisoma* sp., *Biomphalaria glabrata*, and *Physella* sp. In the laboratory the first larval stadium lasted six or seven days; the second stadium, from two to six days; and the third stadium, from five to 11 days ($n = 5$). The larvae made no attempt to reach a drier situation before pupating and all puparia were formed at the water surface in the breeding dishes. The pupal stage lasted from nine to ten days ($n = 4$).

On 25 September, a first generation female that had emerged during the preceding day was placed with two males in a breeding jar. Copulation was not observed until 14 October, but was seen frequently during the next several days. Each copulation lasted from a few minutes to over an hour. The female had not oviposited by 22 October when she was exposed to the light emitted by a 75-watt incandescent lamp. Oviposition first occurred on 27 October, when the female deposited five eggs between 1130 and 1300. Between then and 7 November, 39 eggs were deposited, with the daily count varying from zero to nine. She did not oviposit again until 21 November, but between then and 29 December, she laid an additional 67 eggs. Thus, only 106 eggs were laid by this one female between 27 October and 29 December. Several eggs, especially those laid in December, did not hatch. The female died on 4 February 1959, having lived for 129 days.

Because the laboratory-reared female did not oviposit until nearly a month had

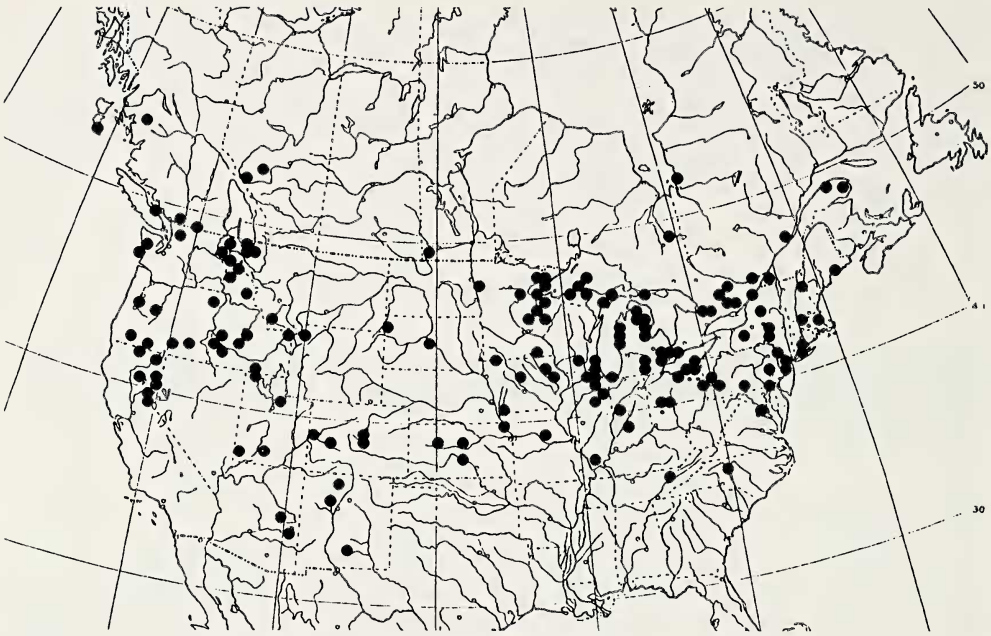

Fig. 10.—Distribution of *T. vicina*.

elapsed from the date of her emergence, it is possible that *T. spreta* has only one generation per year, but additional data are needed before any definite conclusion can be made as to seasonal distribution. Eggs laid by the feral and laboratory-reared females hatched quickly, and neither the larvae nor the pupae showed any unusual delays in development.

Tetanocera vicina Macquart

Macquart, 1843. Diptères exotiques noveaux ou peu connus, 2(3):337.

Tetanocera vicina is restricted to the Nearctic region (Knutson et al., 1986), where it is recorded from New Brunswick west to British Columbia, and south to North Carolina, Tennessee, Kansas, and Arizona (Fig. 10). In central New York and Idaho, adults were swept most abundantly in unshaded vernal marshes. Although several specimens were collected in open marshy land bordering permanent lakes and a very few were swept from wooded swamps and along woodland streams, it appears that *T. vicina* is best adapted to open, vernal marshes containing lush stands of grasses and sedges. In central New York, rearings were obtained from material collected at the Inlet Valley, Floral Avenue, and White Church marshes (Tomkins County). In Idaho, a rearing was initiated from adults taken at a small vernal marsh located near Moscow (Latah County). Additional rearings were obtained from material collected near Kent (Portage County), Ohio.

Adults of *T. vicina* collected in nature during May, June, and early July did not oviposit during the ten to 40 days they were held in the breeding jars, but those taken in August and early September began ovipositing a few days after being confined. Laboratory-reared females remained alive for more than a month before ovipositing, indicating that the eggs had an unusually long maturation

period. One female that emerged on 22 November did not begin ovipositing until 7 January, 46 days later. Another that emerged in early May did not lay her first eggs until late July. It is evident that *T. vicina* is a univoltine species in which the adults emerging in late spring and early summer do not begin ovipositing until late summer and early autumn. In contrast to those of other univoltine species (e.g., *T. loewi*), the eggs of *T. vicina* hatch within a few days. The newly hatched larvae begin feeding on aquatic snails and continue to grow until their activity is slowed and finally stopped by lowering water temperatures. With the return of warm weather and melting of the ice, the larvae again become active and attain their full growth during the late spring. Pupation occurs in late spring, with adults emerging in 18 to 20 days.

The only rearing of this species from adult to adult was initiated from eggs laid on 1 October by two females that were collected on 29 September at the Inlet Valley marsh. All eggs were deposited on the leaves and stems of the moss used as a substrate in the breeding jar. Fifteen larvae hatched in seven to nine days. The aquatic larvae were highly predacious and fed voraciously on a wide variety of nonoperculate aquatic snails. The first larval stadium lasted four to five days; the second, five to six days; and the third, from nine to 12 days ($n = 4$). The only puparium that produced an adult was formed on the surface of shredded peat moss on 29 October. The adult emerged on 16 November, after a pupal period of 18 days.

On 23 August, a second rearing was initiated from eggs laid by two females collected on 18 August at a small vernal marsh located 8.8 km north of Moscow (Latah County), Idaho. Between 23 and 29 August, 166 eggs were deposited followed by death of the female. Of these eggs, 85 were attached to projecting sprigs of peat moss, 59 were placed at various places on the shells of living and dead *Lymnaea* and *Helisoma*, and 22 were laid on the lower 2.5 cm of the glass walls of the breeding jar. Of those eggs placed on peat moss, 35 were clustered together in one compact mass at the tip of a projecting sprig, while the other 50 were scattered over the moss surface. Most eggs laid on shells were placed in the sutures separating the body whorls, but several were attached to the parietal lips or onto convex surfaces. Those laid on the glass walls were scattered, and only rarely were eggs touching each other. Hatching occurred in nine to 14 days, with most larvae emerging in ten to 12 days ($n = 44$). Records were maintained on the number of snails eaten by the first- and second-instar larvae. Each of six first-instar larvae destroyed between six and eight *Gyraulus parvus*, ranging in diameter from 1.3 to 2.9 mm. Two second instar larvae consumed eight and nine *Lymnaea obrussa*, ranging in length from 2.3 to 7.0 mm, respectively. A third-instar larva consumed five *L. obrussa* (5.0–7.0 mm long) before dying. The first larval stadium in this rearing lasted from two to five days; the second, from seven to nine days ($n = 6$). As larvae died before forming puparia, the length of time spent in the third instar could not be determined.

Puparia obtained from larvae collected in nature were frequently formed on peat moss or within empty snail shells. Although a few puparia were formed at the water surface in dishes lacking moss, many larvae in such dishes died, apparently while pupariating. The posterior end of the puparium was only slightly upturned, and it is probable that the larvae either move to the shore or enter hollow stems before pupariating. The fact that puparia were not found in nature, even in marshes where larvae were abundant earlier, is additional evidence that

the larvae leave the water prior to forming puparia. The pupal stage lasted from 18 to 20 days ($n = 8$).

Reared females did not accept males until ten to 15 days after emerging from puparia. Copulation was repeated frequently throughout the life of the females, with each act lasting from a few minutes to over an hour. A female that was collected at the Inlet Valley marsh on 29 September laid 42 eggs before dying on 9 October. Another female that emerged in the laboratory on 21 September produced 27 eggs before dying on 19 February. Feral adults collected in August and September laid from 40 to 81 eggs. A few reared adults remained alive in the breeding jars for as long as 100 days, but most died within 25 days.

In central New York, the first seasonal record for adults was made on 31 May; the latest, on 29 September. In Idaho, the earliest record was made on 19 June; the latest, on 1 October. In both states adults were collected commonly throughout the summer months. Larvae were taken at the White Church marsh on 6 November, at the Inlet Valley marsh on 1 January, and in several marshes between February and early May. Probably both second- and third-instar larvae can overwinter as one of the larvae taken on 6 November was in the earlier instar. Other second-instar larvae were collected during the early spring, but most of those collected in winter and early spring as well as one of the two collected on 6 November were in the third instar. Larvae taken in midwinter and early spring readily attacked, killed, and fed on snails and quickly completed development, but the two taken on 6 November did not feed and died a few days after being brought into the heated laboratory. Although this observation might suggest that the larvae are in diapause during early winter, the rearing of larvae through to pupation from eggs laid during September provides evidence to the contrary.

No parasitoid wasps were obtained from the scores of puparia collected in nature. Perhaps *T. vicina* evades hymenopterous enemies because its larvae develop in seasons when wasp activity is at a minimum.

Discussion

Species comprising the aquatic predator guild possess certain behavioral and morphological features in common. Larvae of all ten species are overt, generalized predators of aquatic pulmonate snails, kill quickly, consume several snails their during larval life, and usually form puparia at the water's surface. The larvae prey on aquatic snails at or near the water's surface and do not forage below the surface to any extent. They lie just beneath the surface film in shallow water, commonly near shorelines, and keep their posterior spiracles in contact with the atmosphere. In general, the larvae are dark in color, have wrinkled integuments, elongate lobes around the posterior spiracular disc, and four well-developed, branching spiracular processes (float hairs) on the posterior spiracles.

Although the guild of aquatic predators in the genus *Tetanocera* is sizeable, consisting of at least ten species in North America, resource partitioning probably reduces competitive interactions. There does not appear to be much partitioning of the trophic axis, as all species are generalized predators of a variety of aquatic pulmonate snails. The spatial axis is partitioned to some extent, as certain species have fairly distinct geographic distributions. *Tetanocera robusta* and *T. obtusifibula* are largely western, *T. spreta* is known only from the central plateau area of Mexico, and *T. annae* is most commonly found in the northeastern states, whereas the remaining six species are more widely distributed.

Table 2.—*Habitat utilization in ten species of malacophagous* Tetanocera.

Species	Habitat
T. annae	Permanent woodland swamps
T. ferruginea	Permanent unshaded marshes
T. latifibula	Permanent unshaded marshes
T. loewi	Vernal woodland pools
T. mesopora	Vernal unshaded marshes
T. montana	Permanent and vernal woodland pools
T. obtusifibula	Vernal unshaded marshes
T. robusta	Permanent unshaded marshes
T. spreta	Vernal unshaded marshes
T. vicina	Vernal unshaded marshes

Differences in habitat occurrence are also recognizable (Table 2). *Tetanocera ferruginea, T. latifibula*, and *T. robusta* are found in unshaded permanent marshes, dominated by herbaceous vegetation, in which water is present throughout the year. In contrast, *T. mesopora, T. obtusifibula, T. vicina*, and probably *T. spreta* occur in more ephemeral marshes that contain water only during the spring and early summer months. Permanently flooded woodland swamps are occupied by *T. annae* and possibly *T. montana*, whereas wooded sites containing only vernal pools that dry up as summer progresses are the home of *T. vicina* and *T. montana*.

Perhaps the niche axis that is most obviously partitioned is the temporal one, as different species have rather specific feeding times and phenologies (Table 3). *Tetanocera obtusifibula* and *T. vicina* are univoltine, overwinter as partly grown larvae in diapause, and do most of their feeding during the autumn and spring months. *Tetanocera latifibula, T. loewi, T. mesopora*, and *T. montana* are also univoltine, but pass the winter as fully embryonated but diapausing eggs. Hatching in those species probably occurs in early spring, and larval feeding is largely completed by late April. In contrast, *T. ferruginea* and *T. robusta* are multivoltine, overwinter as pupae, and have successive generations of larvae feeding throughout the warm season. *Tetanocera annae* is somewhat unusual in that it appears to be univoltine, overwinters as pupae in diapause, and completes its larval life in early summer.

No conclusions can be drawn as to the forces that drove resource partitioning in this guild, but the idea of interspecific competition is an appealing one. One interesting possibility is the concept of the "ghost of competition past" (Connell,

Table 3.—*Phenology of ten species of malacophagous Tetanocera.*

Species	Overwintering stage	Voltinism	Larval feeding time
T. annae	Pupa	Univoltine	Early summer
T. ferruginea	Pupa	Multivoltine	Summer
T. latifibula	"Egg"	Univoltine	Spring
T. loewi	"Egg"	Univoltine	Spring
T. mesopora	"Egg"	Univoltine	Spring
T. montana	"Egg"	Univoltine	Spring
T. obtusifibula	Larva	Univoltine	Spring
T. robusta	Pupa	Multivoltine	Summer
T. spreta	NA	Multivoltine?	NA
T. vicina	Larva	Univoltine	Autumn, spring

1980) which suggests that partitioning resulted from intense competition for resources during times of increased environmental stress. Certainly drought can reduce aquatic habitats dramatically which, in turn, would result in significantly lower snail populations. As a result, competition for one or more limiting resources (habitats, snails) would intensify. Any phenological or habitat shift on the part of *Tetanocera* species would have selective value.

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Specimens of species reared in this study have been deposited in the insect collections of Cornell University and Carnegie Museum of Natural History.

This paper is dedicated to the fond memory of Dr. C. O. Berg, Department of Entomology at Cornell University, who inspired numerous students throughout the world to initiate studies of the biology of the Sciomyzidae.

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